Cross-sectional Investigation of Non-kin Affiliation in Bonobos (*Pan paniscus*)

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Honors Research Thesis
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May 2012

Abstract

Research on captive and wild bonobos (*Pan paniscus*) has provided evidence for strong bonding among adult females and between adult males and females. However, few studies have investigated how association patterns differ between age/sex classes. Here we provide a cross-sectional investigation of affiliative interactions between non-relatives of different age/sex classes in captive bonobos. Patterns of association among adults were similar to those reported from other captive and wild studies. Each of the juvenile/sub-adult females exhibited an affiliation pattern that differed significantly from expected values ($G=73.559$, $p<0.001$; $G=9.336$, $p<0.01$; $G=22.892$, $p<0.001$) and primarily targeted non-related juvenile/sub-adult males and adult females. Unlike juvenile/sub-adult females, juvenile/sub-adult males exhibited greater variation in their pattern of affiliation, where the oldest associated significantly more with adult females ($G=69.760$, $p<0.001$) and the youngest two primarily targeted juvenile/sub-adult females and adult males ($G=53.524$, $p<0.001$; $G=94.536$, $p<0.001$). The infant female initiated affiliation with adult males significantly more than with any other age/sex class ($G=14.616$, $p<0.001$). The infant male rarely initiated affiliation with non-relatives. These variations in patterns of affiliation between age/sex classes may reflect changes in behavioral strategies as individuals age, become more independent, and establish reproductively salient social bonds. Research was supported by The Ohio State University College of Food, Agricultural, and Environmental Sciences Will C. Hauk Endowment fund.

Introduction

Social species tend to direct affiliative behavior toward kin rather than those sharing little or no genetic relation. Hamilton (1964) proposed the theory of kin selection, which explains that natural selection has led to the evolution of a preference for social interactions with relatives because such behavior increases one's inclusive fitness. An organism can promote its genetic representation in the population both directly, through care of its own offspring, and indirectly, by supporting relatives that share some of the same genes. Cooperation among kin is particularly evident in primate species living in multimale-multifemale groups. For example, female white-faced capuchins most frequently form affiliative dyads with maternal sisters and half-sisters (Perry et al., 2008). Not only does the frequency of behaviors differ between relatives versus non-relatives, but the style of behaviors differs as well. When unrelated female Japanese macaques approach each other, they shake their heads, produce specific vocalizations, and smack their lips; this explicit communication is apparently not needed when relatives intend to groom one another (Gouzoules and Gouzoules, 1987). Thus, kin selection is known to shape the dynamic of socially acceptable interactions between any two individuals in some social species.

Kin selection theory does not, however, provide an evolutionary explanation for the occurrence of affiliation between non-relatives. Why might non-kin cooperate? Food, survival, and reproduction are all means through which direct reciprocity or immediate shared benefits can induce unrelated individuals to jointly participate in a given social behavior (Clutton-Brock, 2009). Marked cooperation is seen when meerkats mob potential predators, African wild dogs and lions chase prey, and olive baboons form intersexual friendships (Smuts, 1987; Walters and Seyfarth, 1987; Clutton-Brock, 2009). Because one's social position within a group largely determines the costs and benefits associated with particular behaviors, patterns of non-kin

affiliation likely vary by age and sex. The social structure and direction of sex-biased dispersal of a species are expected to shape the patterns of affiliation among its constituents. To illustrate, in Old World monkeys with matrilineal societies, the most frequent grooming occurs between females because males leave the natal group (Walters, 1987). In contrast, primate species practicing male philopatry exhibit a different pattern of affiliation. Among hamadryas baboons (*Papio hamadryas*), mountain gorillas (*Gorilla beringei beringei*), and chimpanzees (*Pan troglodytes*), unrelated males develop stronger bonds than females (Walters, 1987). This form of intrasexual bonding is likely driven by the female dispersal that characterizes these species.

The bonobo (*Pan paniscus*), a species of great ape closely related to the chimpanzee, is also known to practice female dispersal. Bonobos live in multimale-multifemale societies and have a choice of forming sub-groups with related or unrelated individuals due to a fission-fusion community structure. However, bonobos are distinct from most other male philopatric species in several aspects of their social system. Within and between sexes, an unusually high prevalence of social tolerance is apparent. Bonobos are also unique in that unrelated adult females form affiliative bonds, a rare phenomenon in a species with female-biased dispersal (Parish, 1996). These intrasexual bonds present females with the opportunity for social dominance over males and other females in the group. Due to these differences in social structure, bonobos serve as an ideal species model for the study of patterns of non-kin affiliation in the context of development.

Previous research has begun to reveal some of the patterns inherent in the social dynamic of bonobo societies. In the wild (Hohmann et al., 1999) and captivity (Stevens et al., 2006), mother-son pairs engage in closer association over longer periods of time than any other dyad. This is thought to be an effect of male philopatry. Because males are much more likely to remain in the natal group than females, mothers and sons can both derive greater long-term benefit in the

form of grooming reciprocity and indirect fitness by affiliating with each other than can mothers and daughters (Surbeck et al., 2011). Females that disperse out of their natal group no longer have the opportunity to associate with their mothers or male siblings. Thus, they turn their attention toward resident females in the new group (Furuichi, 1989). Female primates are known to form alliances to cooperatively defend food resources (Wrangham, 1980). This strategy of female intrasexual bonding is most likely to yield the greatest access to resources since females typically hold a majority of the social power in bonobo populations. By eventually becoming established as a central female in the group, a newly-migrated female can ensure that she will have adequate resources for herself and her future offspring.

Observers of both captive (Stevens et al., 2006) and wild (Hohmann et al., 1999) bonobos have found particularly strong male-female bonding among adults. Adult males are expected to invest a great deal of time in the maintenance of these intersexual relationships because the primary limitation to their reproductive success is access to females. In addition, adult males and females form the central part of the dominance hierarchy, and frequent association between adult group members is critical to the stability and structure of the dominance hierarchy in a group. Therefore, juveniles, adolescents, and sub-adults of both sexes utilize behavioral strategies throughout development that reflect their efforts to secure a place within the dominance hierarchy and maximize their social power and genetic representation among the network of group members. For example, intersexual bonds may form between younger individuals and adults of the opposite sex for reproductive reasons. A sub-adult male could direct his attention toward an adult female in an effort to better ensure his reproductive success upon reaching adulthood. The behavior of infant bonobos is often not as complex as that of other age groups. At two years of age, a bonobo spends nearly all of its time in close proximity with its mother and

still rides ventrally on her chest (Kuroda, 1989). Because an infant primarily witnesses behaviors between its mother and other individuals, infant behavior is expected to closely reflect the mother's behavior.

The objectives of this study were to determine whether males and females differ in the patterns of affiliation that they exhibit, and whether their behavioral strategies change as they age. Maternal kin, particularly mothers and sons, were expected to predominantly affiliate with each other. Among non-kin, it was hypothesized that adults and juvenile to sub-adults would invest in intersexual bonds with adults of the opposite sex, infants would mirror the behavior of their mothers, and all individuals would target adult females in affiliation. In addition to these predicted general trends, patterns of affiliation were expected to vary by age and sex if males and females alter their strategies differently as they develop into adults and form reproductively salient intersexual bonds.

Methods

Data Collection Period, Subjects, and Conditions

Behavioral observations of 16 captive bonobos at the Columbus Zoo and Aquarium (CZA) were made between 9:00 AM and 5:00 PM from July 11 to November 8, 2011. Data from a total of 53 days of observations were utilized for analysis. By age and sex, the bonobos present during the study period included eight males, aged 32, 31, 27, 17, 10, 7, 3, and less than 1, and eight females, aged 29, 29, 19, 18, 8, 7, 5, and 1 (Table 1). The above ages are reported according to September 9, 2011, the point in time exactly halfway through the study period. The two oldest males and two oldest females in the group were wild-born. Age/sex classes were defined as infant (aged 0-2), juvenile to sub-adult (between ages 2 and 11), and adult (aged 11 or

older). These distinctions led to an even distribution of sample size across age/sex classes, including four adults of each sex, three juvenile to sub-adults of each sex, and one infant of each sex.

CZA husbandry staff simulated the natural conditions of a fission-fusion society by providing bonobo group members with access to each other at the beginning of each day. Thus, sub-groups were formed based for the most part on individual association preferences. Sub-groups ranged in size from three to nine individuals. All group combinations among the 16 bonobos were possible except for two adult males which could not be housed in the same enclosure due to previous conflict that resulted in significant injury to one of the males. In addition, toward the end of the study period, one of the sub-adult males could not be kept with one of the adult males for the same reason.

Several enclosures were available for housing the bonobos. A large outdoor enclosure, measuring 57.9 meters by 45.7 meters (2,646 square meters), included trees, bushes, a waterfall, an artificial stream, and ropes in the trees on which the bonobos could climb. Two smaller enclosures, each measuring 18.5 square meters, were situated out of sight behind the outdoor region. Three designated viewing areas with glass windows, from which a majority of the observations for this study were made when the focal group was outside, were located around the exhibit. There were also two adjacent indoor enclosures, each measuring 54.8 square meters, from which the bonobos could be observed. These exhibits included varied sizes of playground platforms and bars. From mid July to early August 2011, a construction crew completely redesigned one of these indoor enclosures and erected additional playground equipment in the other. Ancillary space was available behind these indoor enclosures but was out of sight to the observer. These two supplementary enclosures each measured 22.6 square meters.

Behavioral Data Collection Method

Sub-groups were randomly selected for observation, and each sub-group had an equal probability of being selected. The observer then randomly selected a focal individual to be followed for five minutes (Altmann, 1974). One behavioral focal sample was collected for each bonobo in a sub-group before the observer then moved on to the next randomly chosen sub-group. Focal follows were conducted on all bonobos, except for the infant male since he rarely initiated any dyadic interactions. During focal-animal sampling, only the behaviors in which the focal animal participated were recorded. However, if all individuals in a sub-group were visible at any one time, then ad libitum sampling (Altmann, 1974) was utilized. The observer also conducted instantaneous proximity scans of all individuals in a sub-group every 15 minutes.

A focal sample comprised 15-second segments during which all behaviors taking place during that time period were recorded. Due to the general focus of this study, affiliative behaviors were of the most interest, but behaviors categorized as aggressive/agonistic, intervention, and submissive were also recorded (Appendix A). The ethogram (adapted from Boose, 2009) defined affiliation as instances in which any two individuals were proximate, and at least one individual was engaged in affiliative behavior toward the other. Intraobserver reliability tests for the recording of behaviors and proximity estimation were completed throughout the study period, using 95% as the reliability threshold.

Statistical Analyses

Data were entered into matrices, and software was used to generate dendrograms, which were analyzed to determine the closeness of interactions between any two individuals in terms of

affiliation and spatial proximity. G-tests for goodness-of-fit were performed on the counts of affiliative behavior among non-kin to determine significance in the distribution of the data.

Results

A total of 1,950 affiliative behaviors and 241 agonistic behaviors were recorded from July 11 to November 8, 2011 (Table 2). Grooming was the most frequent affiliative behavior recorded, comprising 49.74% (970/1,950) of all observed affiliation. The remainder of the affiliative behavior category consisted of 27.54% (537/1,950) play, 6.26% (122/1,950) touching, 6.21% (121/1,950) sociosexual behavior, 5.33% (104/1,950) rough and tumble play, 4.41% (86/1,950) copulation, and 0.51% (10/1,950) embracing.

Of the agonistic behaviors, physical contact aggression was the most frequent, making up 30.71% (74/241) of the category. The rest of the agonistic behavioral category, including associated intervention and submissive behaviors, contained 28.63% (69/241) display behavior, 17.43% (42/241) chasing, 7.47% (18/241) pushing, 5.39% (13/241) displacing, 4.98% (12/241) pestering, and 5.39% (13/241) other, which encompassed avoiding, charging, and swinging at target.

Of the 1,950 observed affiliative behaviors, 1,844 were utilized for analysis. The 106 behaviors excluded from data analysis were removed because the observer recorded these behaviors on days during which at least one of the indoor exhibits was undergoing construction. This construction restricted the opportunity for the bonobos to form new sub-groups, so all observations of groups that were clearly affected by the construction were removed from the data set to prevent the possibility of bias. The days for which data were removed due to the

occurrence of construction included July 19, 20, 25, 28, and 29, August 2, 4, and 5, and September 8, 2011.

The 1,844 non-biased counts of affiliative behavior (Table 3) were used to generate a dendrogram of affiliation between all 16 bonobos, including maternal kin (Figure 1). Of the four maternal groups (at least two maternally-related individuals required for a maternal group) at the Columbus Zoo, all members of each group more closely affiliated with each of their maternal relatives than any other individual, with one exception. BI, a ten year old sub-adult male, was more closely grouped with the maternal group consisting of L and JT than with his own maternal group.

All counts of affiliation between maternally-related individuals were removed from the matrix in Table 3, resulting in 1,128 counts of affiliative behavior, to generate a dendrogram of affiliation between non-kin (Figure 3). The closest affiliative pair according to this dendrogram contained Gi and Je, a juvenile female and juvenile male, respectively. The behavioral trends evident in this dendrogram are further discussed in numerical form in the G-test for goodness-of-fit results below.

A total of 633 spatial proximity scans were collected during the study period, but only 508 scans were utilized for data analysis due to the abovementioned construction on the indoor exhibits. The 508 proximity scans (Table 4) recorded for the various sub-group compositions (Table 5) throughout the study period were used to generate a dendrogram of spatial proximity, including proximity counts between maternal kin (Figure 2). Of the four maternal groups, all members of three maternal groups more closely affiliated with each of their maternal relatives than any other individual, with one exception. BI, the ten year old sub-adult male mentioned above, was most closely grouped with JT, a sub-adult female. The only maternal group not

clustered together on the proximity dendrogram consisted of L and JT, an adult female and her daughter, respectively.

All proximity counts between maternally-related individuals were removed from the matrix in Table 4 to generate a dendrogram of spatial proximity for non-kin (Figure 4). According to this dendrogram, the closest pair of bonobos in terms of proximity consisted of J and T, two adult males. The next closest individual to this pair was M, another adult male.

Of the 1,844 counts of affiliative behavior analyzed in the dendrogram, 190 counts were recorded without direction because the observer could not distinguish the initiator of the behavior. Removing these non-directional counts resulted in a matrix of 1,654 counts of directional affiliative behavior among all bonobos (Table 6). To examine patterns of non-kin affiliation in the data, individual recipients of behavior were grouped by age/sex class, and all counts of affiliation between maternally-related individuals were removed from the data set, resulting in 971 directional affiliative behavior counts between non-kin (Table 7). Furthermore, the individual initiators of these affiliative behaviors were grouped by age/sex class to create a concise table of non-kin affiliation for analysis with G-tests for goodness-of-fit (Table 8). The percentage of affiliation directed toward each age/sex class by each age/sex class was also calculated for analysis (Table 9).

When examining non-kin affiliation by age/sex class, adult females ($G = 7.34$, $p < 0.05$) and adult males ($G = 24.95$, $p < 0.001$) targeted adults of both sexes (Table 8). Juvenile to sub-adult females ($G = 71.15$, $p < 0.001$) primarily targeted unrelated juvenile to sub-adult males and adult females (Table 8). Among juvenile to sub-adult males, the oldest ($G = 69.76$, $p < 0.001$) affiliated significantly more with unrelated adult females, while the youngest two ($G = 53.52$, $p < 0.001$; $G = 94.54$, $p < 0.001$) targeted unrelated juvenile to sub-adult females and adult males

(Table 7 and Figure 5). The infant female ($G=14.62$, $p<0.001$) initiated affiliation with adult males significantly more than with any other age/sex class, and the infant male rarely initiated affiliation with non-relatives (Table 8).

Discussion

The results of this study provide strong evidence that affiliation and association among the Columbus Zoo bonobo population follow the line of maternal kinship. The effect of maternity was so powerful that D, a 17 year old male who was the dominant male at the time, more closely affiliated and positioned himself spatially with his 29 year old mother, seven year old half-sibling, and one year old full sibling than any unrelated bonobo in the group. Such pronounced mother-son bonding has been well documented in previous studies of bonobos and has been described as mutually beneficial to the mother and son in terms of indirect fitness (Surbeck et al., 2011). One male bonobo in the Columbus Zoo group did not identify most closely with his mother and siblings in the affiliation and association dendrograms. This ten year old sub-adult male, BI, was instead grouped most closely in affiliation with JT and her mother L, eight year old and 29 year old females, respectively. Beyond L and JT, however, BI was clustered more closely with his maternal group than any other bonobos. It is important to note that BI was in the process of replacing D as the dominant male of the group during the study period. Surbeck et al. (2012) found that high-ranking male bonobos were most likely to have established amicable intersexual relationships with non-kin. Because BI was nearly the highest-ranking male bonobo at the time of observations, he may have been maximizing his efforts to build relationships with unrelated females in the group for reproductive and political benefits, while still maintaining affiliative ties with his mother and siblings for additional support.

Among non-kin, the two age/sex classes with which adult females most affiliated were adult females and adult males. Similarly, adult males affiliated with other adult males and adult females more than any other age/sex class. The intersexual bonding evident in these data agrees with the findings of previous research on bonobos (White, 1996). However, a notable difference between the data from this study and that of previous studies (Hohmann et al., 1999; Stevens et al., 2006) is that both adult males and females exhibited slightly stronger intrasexual than intersexual bonding. Hohmann et al. (1999) found that male-female dyads were longer lasting than female-female dyads in wild bonobos, and Stevens et al. (2006) concluded that male-male bonds were particularly weak in comparison to intersexual bonds. One potential explanation for the prevalence of intrasexual affiliation in this study involves the four wild-born individuals (T, J, L, and S) that were first brought to the Columbus Zoo as the founders of this captive population. This pair of males and pair of females were responsible for a majority of the intrasexual affiliation observed in this study, and much of this affiliation was mutually directed within each of these two pairs. Thus, the existence of well-established friendships between the two adult males over 30 years old and the two 29 year old adult females at the Columbus Zoo could be responsible for the marked intrasexual affiliation seen in the data.

The strong intrasexual bonding seen among unrelated adults of both sexes could reflect an attempt to maintain or increase social rank. As in the T-J pair and L-S pair mentioned above, forming a long-term friendship with an adult of the same sex leads to greater chances of successfully defending one's social rank or gaining more social power and resources, due to the reliable support of an ally. In contrast to the political aspect of intrasexual bonding, the observed intersexual bonding between unrelated adults may indicate an attempt to maximize reproductive success. The unique social system of bonobos, however, presents an additional reason for

intersexual bonding. Female bonobos are the source of social power in bonobo society (Parish, 1996), so attempts by males and females to affiliate with adult females may be driven by the intent to increase one's political power in the group and consequently gain access to more resources. The power held by adult female bonobos is the most likely reason for the high level of affiliation that the juvenile to sub-adult females directed toward the adult females in this study. This finding corresponds to Furuichi's (1989) discovery that, in the wild, migrating females seek out resident adult females in the new group to which they have transferred. By quickly forming friendships with the powerful females of a particular group, newly-arrived females can begin to gradually establish themselves as central group members.

In this study, juvenile to sub-adult females spent more time affiliating with juvenile to sub-adult males than with adult females. The strong intersexual bonding of bonobos (White, 1996), extended to a younger age group, is a likely explanation for this finding. Juvenile to sub-adult females may target similarly-aged individuals of the opposite sex in an attempt to secure reproductive bonds before reaching adulthood. Ga and Je, the two youngest juvenile to sub-adult males in this study, may have primarily targeted juvenile to sub-adult females for the same reason. One of the most noteworthy findings of this cross-sectional study was that BI, the oldest individual in the juvenile to sub-adult male age/sex class, drastically differed in his pattern of affiliation as compared to the two younger males in his age/sex class. Rather than focus his affiliative behavior on juvenile to sub-adult females and adult males, as Ga and Je did, BI targeted adult females and juvenile to sub-adult males in his affiliation. Whether this distinct pattern of affiliation exhibited by BI is an idiosyncrasy of BI's personality and/or social position, or whether this radical difference in affiliation patterns between juvenile and sub-adult males is also apparent in other bonobo populations, cannot be answered at present due to the cross-

sectional scope of this study but remains an essential question to be addressed in future studies. Regardless, BI's age and social position in the group may have allowed BI to derive the greatest reproductive and political benefit by affiliating primarily with adult females. It is worth investigating, via longitudinal studies, whether sub-adult male bonobos nearing adulthood adjust their behavioral strategies to target older females for social bonding, and whether these bonds are driven by an attempt to enhance one's reproductive success or one's political power, or both.

It was predicted that the infants would display a pattern of affiliation that reflected that of their mothers. The infant male initiated too few affiliative behaviors for reliable conclusions to be made with statistical analysis. The infant female, MR, engaged in more affiliation than the infant male. She targeted adult males, in contrast to the adult females that her mother, S, favored. It is possible that this stronger preference for adult males reflects an attempt by MR to interact with males who could potentially be her father. The promiscuous nature of mating in bonobos has led researchers to believe that bonobos are uncertain of paternity (Kuroda, 1989). Hence, paternal kin were not considered kin in the statistical analysis of this study. The sample size of interactions between fathers and actual and potential offspring was not large enough in this data set to perform G-tests for goodness-of-fit. However, a basic analysis of affiliation between potential and actual paternal kin did not demonstrate any evidence that the Columbus Zoo bonobos have knowledge of paternity. Further investigation of this captive population and other bonobo populations will eventually lead to conclusive evidence of whether bonobos have at least a probabilistic idea of paternity, or none at all. Future research may be able to elucidate the question of paternity in bonobos by collecting longitudinal data and examining whether the adult males that mated most frequently with an adult female just before the conception of an infant,

subsequently affiliated more closely with that infant than did other adult males who had a lesser probability of being the father of the infant.

Conclusions

The strongest affiliation and association observed in the Columbus Zoo bonobo population occurred along lines of maternal kin. Males and females were found to engage in differing patterns of non-kin affiliation, especially among the juvenile to sub-adult age group. Behavioral strategies also changed with age in both males and females, based on the cross-sectional analysis of this study. Within the juvenile to sub-adult male age/sex class, a drastic difference in affiliation by age was apparent. The ten year old male targeted adult females in affiliation to a much greater extent than did the seven year old and three year old males. Further research of a longitudinal design could clarify whether such a radical shift in behavioral strategy from age seven to ten consistently occurs among male bonobos. In sum, the observed variations in patterns of affiliation between age/sex classes may reflect changes in behavioral strategies as individuals age, become more independent, and establish reproductively salient social bonds.

Implications

The bonobo remains a fairly enigmatic species compared to other great apes and primates in general. By conducting basic research on bonobos, as in this study, we can begin to understand how the unique ecological factors faced by wild bonobos have shaped the social structure and behavior of this species since its divergence from chimpanzees approximately two million years ago. Continued comparisons among bonobos, chimpanzees, humans, and other primates will eventually lead to a comprehensive understanding of the many variables that

contributed to the evolution of these closely related species with both similar and distinct behavioral tendencies. A more complete scientific perspective of bonobos will also help guide conservation efforts on behalf of this endangered species of great ape.

Acknowledgements

We gratefully acknowledge Audra Meinelt, Kelly Vineyard, Shannon Morarity, Shelly Roach, and the entire African Forest staff and docents at the Columbus Zoo and Aquarium for providing institutional support and permitting the collection of behavioral observations. We thank Dr. Frances White and Klaree Boose for their assistance with statistical analysis of the data and for offering insightful suggestions for this paper. We also thank Dr. Pasha Lyvers Peffer for providing valuable comments. This research was supported by the Ohio State University College of Food, Agricultural, and Environmental Sciences Will C. Hauk Endowment fund.

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Tables & Figures

Table 1. Columbus Zoo and Aquarium *Pan paniscus* population (adapted from Boose, 2009).

Subject	Class	Sex	Date of Birth	Offspring of[2]:
S (Susie)	Adult	F	1982[1] wild	
L (Lady)	Adult	F	1982[1] wild	
AN (Ana Neema)	Adult	F	1992 captivity	
U (Unga)	Adult	F	1993 captivity	
T (Toby)	Adult	M	1979[1] wild	
J (Jimmy)	Adult	M	1979[1] wild	
M (Maiko)	Adult	M	1984 captivity	
D (Donnie)	Adult	M	1993 captivity	Susie and Jimmy
JT (Jo-T)	Juvenile to sub-adult	F	2002 captivity	Lady
Lo (Lola)	Juvenile to sub-adult	F	2004 captivity	Susie and Toby
Gi (Gilda)	Juvenile to sub-adult	F	2006 captivity	Ana Neema
BI (Bila Isia)	Juvenile to sub-adult	M	2001 captivity	Ana Neema
Ga (Gander)	Juvenile to sub-adult	M	2003 captivity	Unga
Je (Jerry)	Juvenile to sub-adult	M	2008 captivity	Unga and Donnie
MR (Mary Rose)	Infant	F	2010 captivity	Susie and Jimmy
W (Wilbur)	Infant	M	2010 captivity	Ana Neema and Donnie

[1]estimated age

[2]parents listed only if currently residing at the Columbus Zoo

Table 2. Total count and percentage of affiliative and agonistic/intervention/submissive behaviors observed during the study period.

Behavior Category	Behavior	Total Number	Percentage of Category
Affiliative	Grooming	970	49.74
	Play	537	27.54
	Rough and Tumble Play	104	5.33
	Sociosexual Behavior	121	6.21
	Copulation	86	4.41
	Touching	122	6.26
	Embracing	10	0.51
	Total	1950	100
Agonistic	Physical Contact Aggression	74	30.71
	Display Behavior	69	28.63
	Chasing	42	17.43
	Pushing	18	7.47
	Displacing	13	5.39
	Pestering	12	4.98
	Other*	13	5.39
	Total	241	100

*Includes Avoiding, Charging, and Swinging at Target

Table 3. Matrix of 1,844 observed counts of directional and non-directional affiliative behavior, directed toward each individual by individual.

	AN	BI	D	Ga	Gi	J	Je	JT	L	Lo	M	MR	S	T	U	W
AN	/	39	6	3	76	0	4	32	2	3	1	2	13	0	4	53
BI		/	0	14	14	0	49	37	12	10	1	3	12	2	22	12
D			/	14	6	0	40	7	8	11	0	25	21	3	5	1
Ga				/	20	18	66	24	17	33	19	2	0	9	45	0
Gi					/	1	86	18	9	19	5	14	10	5	12	38
J						/	35	0	11	17	6	11	9	30	9	0
Je							/	28	6	60	12	24	4	31	65	6
JT								/	31	11	0	3	10	0	12	15
L									/	9	4	11	13	3	1	3
Lo										/	17	63	96	5	12	2
M											/	4	4	5	1	0
MR												/	61	17	0	15
S													/	10	3	0
T														/	1	1
U															/	0
W																/

Table 4. Matrix of observed counts of any two individuals observed in close proximity (3 meters or less), based on 508 spatial proximity scans.

	AN	BI	D	Ga	Gi	J	Je	JT	L	Lo	M	MR	S	T	U	W
AN	/	68	9	15	102	2	20	54	18	15	9	15	20	2	20	190
BI		/	0	31	58	3	42	59	23	12	13	1	3	3	36	65
D			/	9	7	0	14	21	16	38	0	47	44	1	14	9
Ga				/	15	25	70	12	29	23	17	8	8	31	69	14
Gi					/	4	32	34	21	25	7	14	19	3	24	102
J						/	20	0	24	21	39	18	20	84	20	2
Je							/	28	4	20	16	9	10	21	118	20
JT								/	19	29	4	30	28	0	20	53
L									/	35	12	21	16	18	6	16
Lo										/	15	72	72	13	16	15
M											/	15	15	39	15	9
MR												/	135	23	4	16
S													/	22	4	19
T														/	29	2
U															/	20
W																/

Table 5. Matrix of the number of days any two individuals were observed in the same enclosure during the study period.

	AN	BI	D	Ga	Gi	J	Je	JT	L	Lo	M	MR	S	T	U	W
AN	/	35	6	4	36	4	7	25	14	9	4	9	9	3	7	40
BI		/	2	10	34	5	13	24	13	6	8	5	5	5	13	35
D			/	10	8	0	13	14	13	26	0	24	24	3	13	6
Ga				/	10	12	28	6	8	10	11	3	3	15	28	4
Gi					/	3	13	27	15	14	2	10	10	1	13	36
J						/	9	1	8	6	28	6	6	31	9	4
Je							/	8	5	11	9	6	6	12	37	7
JT								/	9	17	4	14	14	1	8	25
L									/	17	7	17	17	9	5	14
Lo										/	4	29	29	4	11	9
M											/	4	4	29	9	4
MR												/	35	5	6	9
S													/	5	6	9
T														/	12	3
U															/	7
W																/

Figure 1. Dendrogram of 1,844 affiliative interactions observed among all bonobos, including maternal kin. Red brackets designate maternal groups.

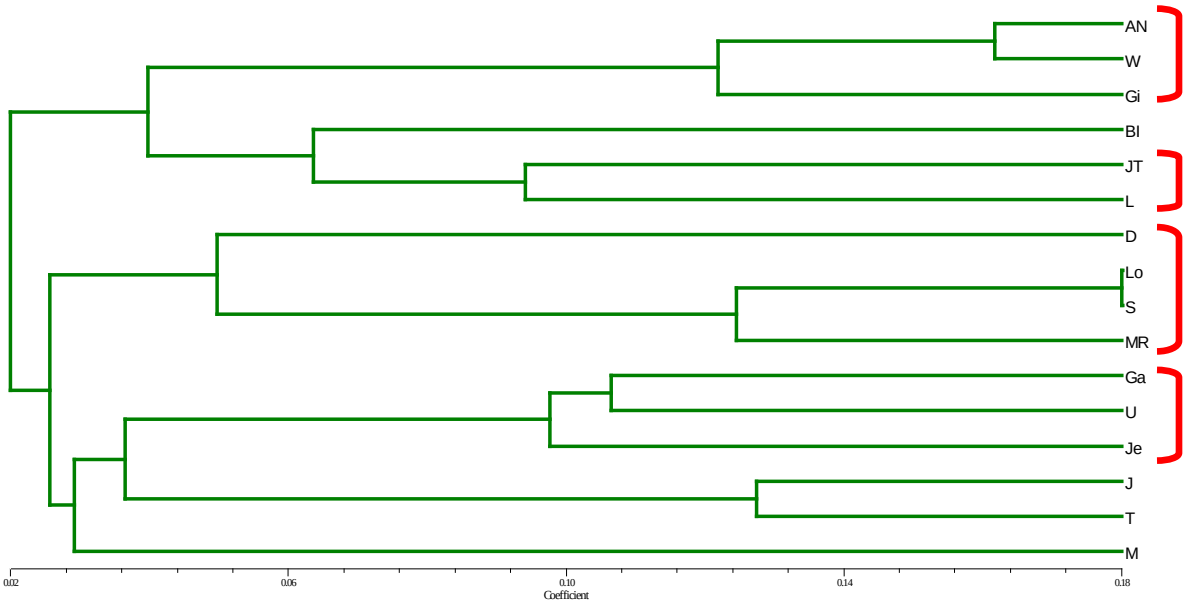


Figure 2. Dendrogram of 508 spatial proximity scans, including proximity counts between maternal kin. Red brackets designate maternal groups.

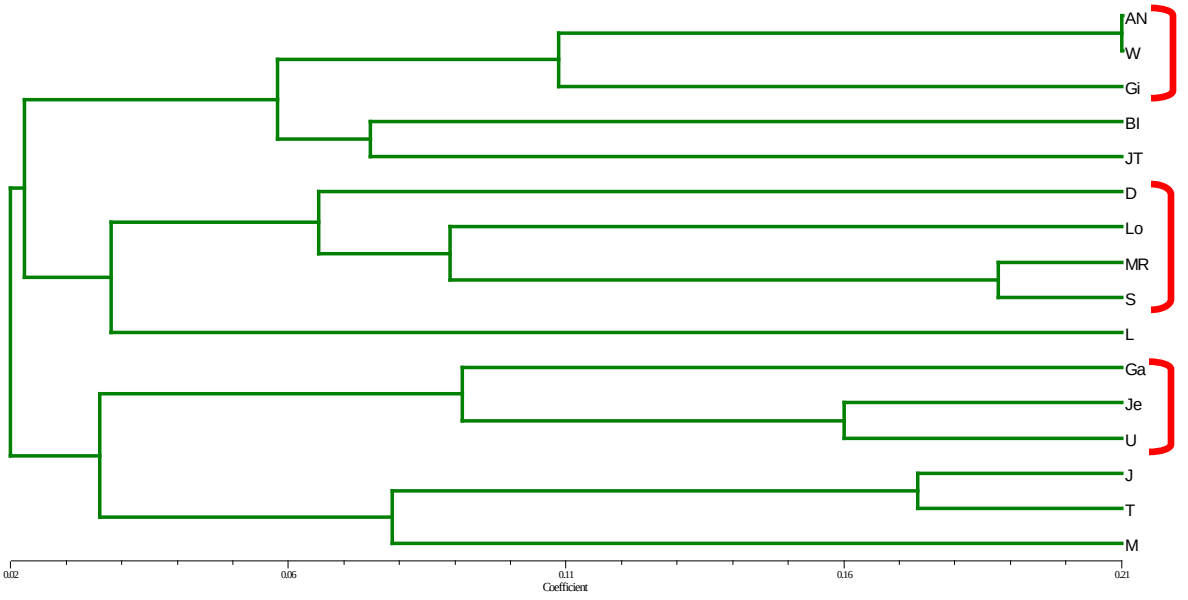


Figure 3. Dendrogram of 1,128 affiliative interactions observed among non-kin (i.e., non-maternally-related individuals).

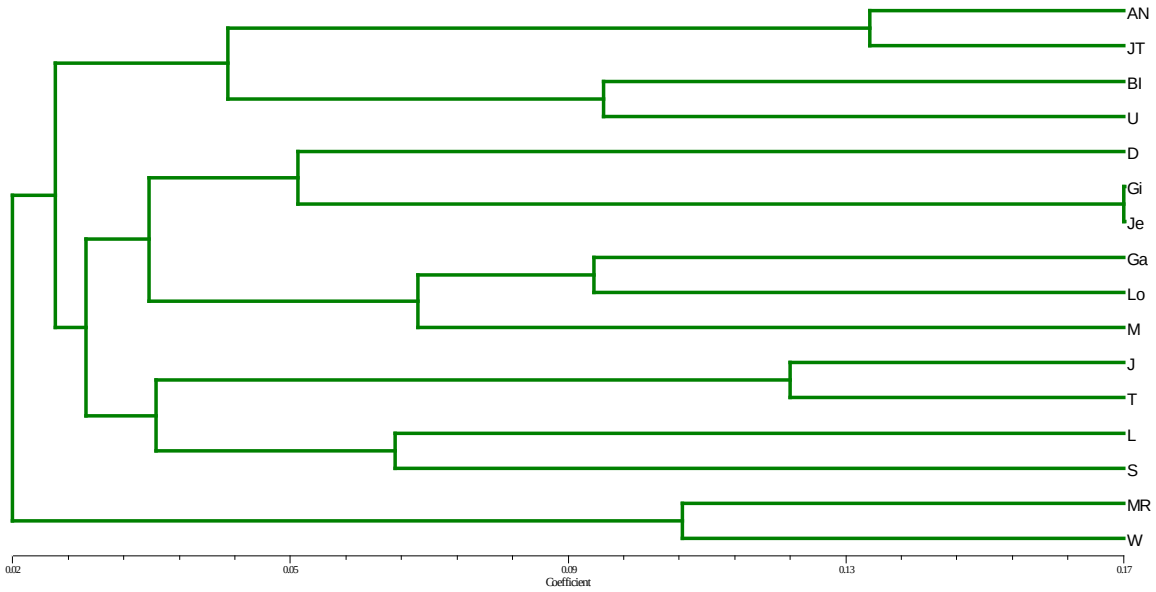


Figure 4. Dendrogram of 508 spatial proximity scans, excluding all proximity counts between maternally-related individuals.

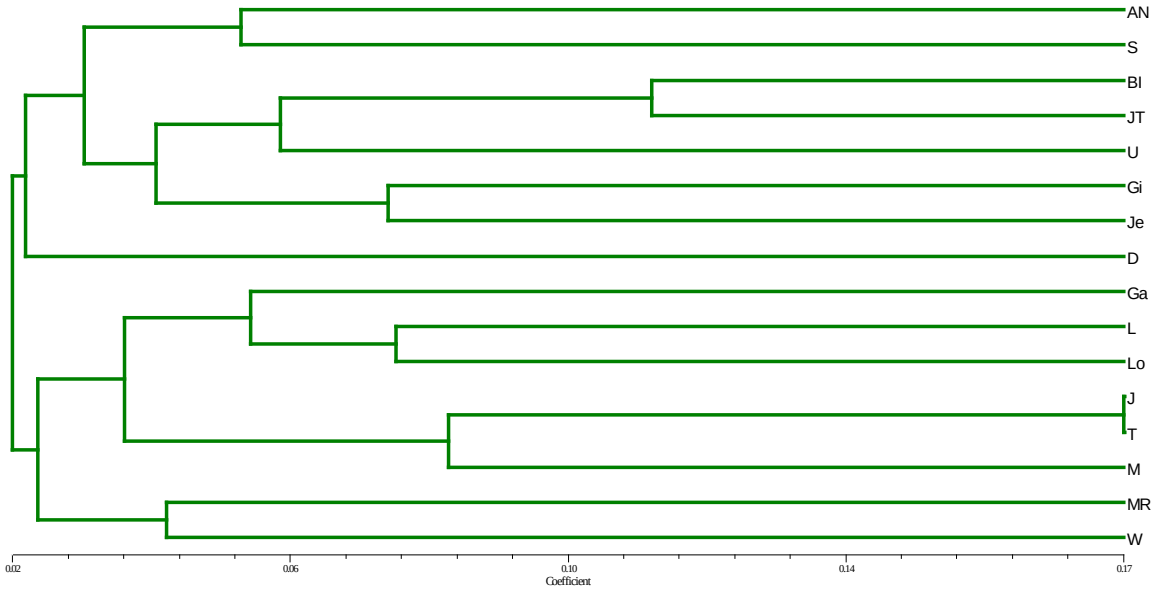


Table 6. Matrix of 1,654 observed counts of directional affiliative behavior, directed toward each individual by individual.

	AN	BI	D	Ga	Gi	J	Je	JT	L	Lo	M	MR	S	T	U	W	Total
AN	/	21	3	0	32	0	0	5	0	1	1	2	4	0	1	44	114
BI	18	/	0	5	8	0	16	7	9	1	0	0	3	0	17	6	90
D	2	0	/	4	1	0	8	3	4	2	0	3	8	1	3	0	39
Ga	2	5	9	/	13	13	32	11	10	23	11	1	0	7	18	0	155
Gi	41	3	3	3	/	1	19	11	5	5	4	3	5	1	12	28	144
J	0	0	0	3	0	/	0	0	5	8	3	1	4	12	5	0	41
Je	4	29	25	23	49	33	/	12	4	36	11	18	4	20	28	6	302
JT	24	28	4	5	5	0	10	/	15	2	0	3	5	0	10	14	125
L	0	3	4	3	1	6	2	16	/	4	1	3	8	0	1	3	55
Lo	1	8	7	6	8	8	15	4	5	/	7	28	45	1	11	2	156
M	0	0	0	8	1	2	0	0	2	7	/	0	1	2	1	0	24
MR	0	1	20	1	6	8	2	0	8	27	3	/	17	7	0	8	108
S	9	2	13	0	2	5	0	3	5	51	0	44	/	2	3	0	139
T	0	2	2	2	4	18	7	0	3	4	3	7	8	/	1	0	61
U	2	2	2	27	0	4	37	0	0	1	0	0	0	0	/	0	75
W	8	6	1	0	7	0	0	1	0	0	0	2	0	1	0	/	26
																	1654

Table 7. Matrix of 971 observed counts of non-kin directional affiliative behavior, directed toward each age/sex class by individual. G values and p-values were obtained from G-tests for goodness-of-fit. AF = Adult Female, AM = Adult Male, JSF = Juvenile to Sub-adult Female, JSM = Juvenile to Sub-adult Male, IF = Infant Female, IM = Infant Male.

	AF	AM	JSF	JSM	IF	IM	Total	G value	p-value
AN	5	4	6	0	2	/	17	9.22	p<0.01
L	9	11	5	8	3	3	39	0.16	p=0.92
S	17	7	5	2	/	0	31	19.54	p<0.001
U	2	6	1	2	0	0	11	7.49	p<0.05
D	9	1	4	12	/	0	26	16.19	p<0.001
J	14	15	8	3	1	0	41	16.60	p<0.001
M	4	4	8	8	0	0	24	11.13	p<0.01
T	12	23	8	11	7	0	61	20.44	p<0.001
Gi	22	9	16	22	3	/	72	22.89	p<0.001
JT	39	4	7	43	3	14	110	73.56	p<0.001
Lo	17	16	12	29	/	2	76	9.34	p<0.01
BI	29	0	8	21	0	/	58	69.76	p<0.001
Ga	12	40	47	5	1	0	105	53.52	p<0.001
Je	12	89	97	29	18	6	251	94.54	p<0.001
MR	8	18	6	4	/	8	44	14.62	p<0.001
W	0	2	1	0	2	/	5	7.37	p<0.05
							971		

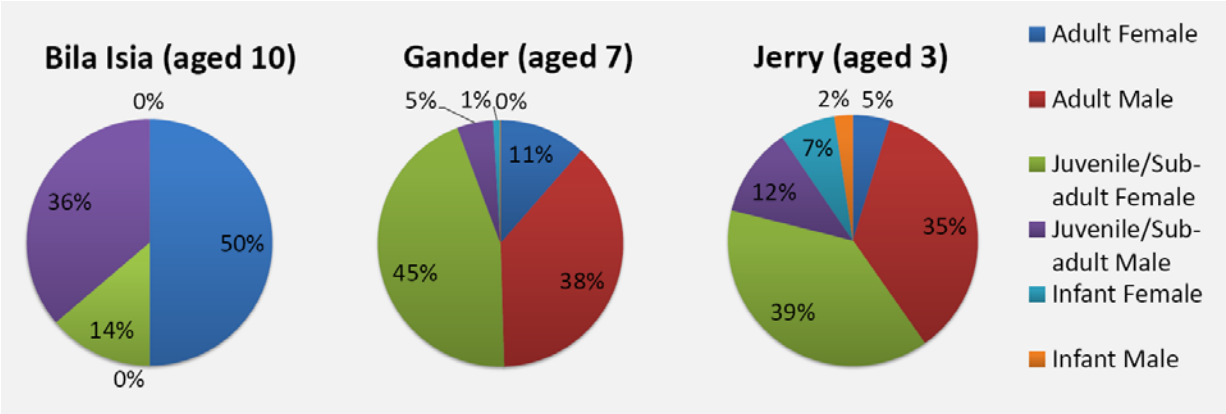
Table 8. Matrix of 971 observed counts of non-kin directional affiliative behavior, directed toward each age/sex class by age/sex class. G values and p-values were obtained from G-tests for goodness-of-fit. AF = Adult Female, AM = Adult Male, JSF = Juvenile to Sub-adult Female, JSM = Juvenile to Sub-adult Male, IF = Infant Female, IM = Infant Male.

	AF	AM	JSF	JSM	IF	IM	Total	G value	p-value
AF	33	28	17	12	5	3	98	7.34	p<0.05
AM	39	43	28	34	8	0	152	24.95	p<0.001
JSF	78	29	35	94	6	16	258	71.15	p<0.001
JSM	53	129	152	55	19	6	414	89.92	p<0.001
IF	8	18	6	4	/	8	44	14.62	p<0.001
IM	0	2	1	0	2	/	5	7.37	p<0.05
							971		

Table 9. Matrix of percentages of non-kin directional affiliative behavior directed toward each age/sex class by age/sex class. AF = Adult Female, AM = Adult Male, JSF = Juvenile to Sub-adult Female, JSM = Juvenile to Sub-adult Male, IF = Infant Female, IM = Infant Male.

	AF	AM	JSF	JSM	IF	IM	Total %
AF	33.67	28.57	17.35	12.25	5.10	3.06	100.00
AM	25.66	28.29	18.42	22.37	5.26	0	100.00
JSF	30.23	11.24	13.57	36.43	2.33	6.20	100.00
JSM	12.80	31.16	36.71	13.29	4.59	1.45	100.00
IF	18.18	40.91	13.64	9.09	0	18.18	100.00
IM	0	40	20	0	40	0	100.00

Figure 5. Percentage of affiliative behaviors directed toward non-kin by the three juvenile to sub-adult males (58, 105, and 251 total events, respectively).



Appendix A: *List of Behaviors*

I. Proximity (How close individuals are in space)

1. Proximate – within three meters of another individual

II. Affiliative Behaviors

1. Sociosexual Behavior – all non-copulatory genital-genital contact between individuals.
2. Copulation – intromission of an individual male's penis into the vagina of a female, usually accompanied by thrusting movements.
3. Play – prolonged pattern of affiliative touching resulting in the appearance of a 'play face' on individual participants.
4. Rough and Tumble Play – prolonged pattern of affiliative touching characterized by more erratic and forceful movements than Play, but still resulting in the appearance of a 'play face' on individual participants.
5. Grooming – prolonged pattern touching where one individual runs their fingers and mouth over the hair and skin of another individual, sometimes removing excess skin and debris.
6. Embracing
7. Touching

III. Aggressive/Agonistic Behaviors (Kano, 1992)

1. Chasing – tensed running toward another individual over a long distance, no shorter than 5 meters.
2. Charging – tensed running toward another individual over a short distance, no longer than 5 meters.
3. Physical Contact Aggression – intentional hitting, kicking, slapping, dragging, pulling, pushing or biting of a body part of another individual.
4. Threaten – tensed gesticulating or very short (less than 3 meters) charge behavior directed at an individual.
5. Swinging at target – intentional movement (of body or object) past an individual resulting in brief physical contact.
6. Display behavior directed at another individual.
7. Displacing – inserting oneself into the physical location of another individual, forcing that individual to move to a new location.
8. Pushing – forcing the trajectory of another individual without making direct contact.

*Pilo-erection usually occurred during all aggressive behaviors.

IV. Intervention Behaviors

1. Interposition (defined as a third individual placing themselves in between the individuals engaged in any type of dyad: aggressive or affiliative).
2. Pestering behavior (defined as a repeated mild agonistic behavior pattern) directed at one or both dyad participants.
3. Display behavior directed at one or both dyad participants.
4. Agonistic behavior directed at one or both dyad participants.

V. Submissive Behaviors (Kano, 1992)

1. Crouching – individual makes a 'bowing' motion in response to aggression.
2. Screaming – high-pitched, tense, loud vocalization in response to aggression.
3. Teeth-baring – individual curls back lips to expose both top and bottom teeth, similar to a 'smile' in response to aggression.
4. Fleeing – individual runs away, leaving proximity of an aggressor, in response to aggression.
5. Avoiding – individual changes locomotion trajectory and does not enter proximity of another individual. May or may not occur in response to aggression.